



Factors that affect heat production in lactating Jersey cows

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ABSTRACT

Heat production (HP) represents a major energy cost in lactating dairy cows. Better understanding of factors that affect HP will improve our understanding of energy metabolism. Our objective was to derive models to explain variation in HP of lactating Jersey cows. Individual animal-period data from 9 studies ($n = 293$) were used. The data set included cows with a wide range (min to max) in days in milk (44–410) and milk yield (7.8–43.0 kg/d). Diets included corn silage as the predominate forage source, but diets varied (min to max on DM basis) in crude protein (CP; 15.2–19.5%), neutral detergent fiber (NDF; 35.5–43.0%), starch (16.2–31.1%), and crude fat (2.2 to 6.4%) contents. Average HP was (mean \pm standard deviation) 22.1 ± 2.86 Mcal/d, or $28.1 \pm 3.70\%$ of gross energy intake. Eight models were fit to explain variation in HP: (1) dry matter intake (DMI; INT); (2) milk fat, protein, and lactose yield (MILKCOMP); (3) INT and milk yield (INT+MY); (4) INT and MILKCOMP/DMI (INT+MILKCOMP); (5) mass of digested NDF, CP, and starch (DIG); (6) INT and digested energy (INT+DE); (7) INT and NDF, CP, and starch digestibility (INT+DIG); or (8) INT+MILKCOMP model plus urinary N excretion (INT+MILKCOMP+UN). For all HP models, metabolic body weight was included. All models were derived via a backward elimination approach and included the random effects of study, cow, and period within block within study. The INT models adequately explained variation in HP with a nonrandom effect-adjusted concordance correlation coefficient of 0.84. Similar adjusted concordance correlation coefficients (0.79–0.85) were observed for other HP models. The HP associated with milk protein yield and supply of digestible protein was greater than other milk production and nutrient digestibility variables. The HP associated with urinary N excretion was 5.32. Overall, HP can

be adequately predicted from metabolic body weight and DMI. Milk component yield, nutrient digestibility, or urinary N excretion explained similar variation as DMI. Coefficients for milk protein and protein digestion suggest that digestion and metabolism of protein and synthesis of milk protein contribute substantially to HP of a dairy cow.

Key words: energy, indirect calorimetry, empirical model

INTRODUCTION

Heat in animals is generated from the catabolism of organic compounds. According to the laws of thermodynamics, heat generated from reactions in the body is equal to the difference in chemical energy between all substrates and products in a reaction (Kleiber, 1975). In lactating Jersey cows, heat production (**HP**) accounts for 25 to 32% of the gross energy (**GE**) intake (Drehmel et al., 2018; Judy et al., 2018; Reynolds et al., 2019). Heat production can be categorized into NE_M —the basal energy expenditure of an animal—and heat increment (**HI**)—the HP that is associated with digestion and metabolism of food (NRC, 1981). Because HI represents a loss of energy and is the difference between ME and NE_L , changes in HI may affect net milk production and tissue energy accretion of a dairy cow. Energetic efficiency, HP, and HI are affected by plane of production (Belyea and Adams, 1990), forage inclusion (Reynolds et al., 1991), and N intake above requirements (Tyrrell et al., 1970; Reed et al., 2017). Various factors are likely to influence HP and HI, and quantification of these may improve our ability to estimate NE_L of diets.

We recently observed that the NRC (2001) model underestimated dietary NE_L content compared with measured NE_L , when NE_M was assumed to equal 0.080 Mcal per metabolic BW ($BW^{0.75}$, **MBW**; Morris et al., 2020a). Furthermore, it has been shown that the efficiency of converting ME into NE_L (denoted as k_L) is affected by diet (Moraes et al., 2015; Morris et al., 2020b). Historically, the NE_L system assumed a constant or near

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constant k_L (Moe et al., 1972; NRC, 2001). A recent analysis of indirect calorimetry data from the 1960s through the 1990s reported that k_L ranged from 0.60 to 0.70 and was associated with heart rate, milk yield, and dietary crude fat (Moraes et al., 2015). Biologically, k_L is likely dependent upon the substrates utilized and products formed (Baldwin, 1995). For example, HI has been reported to be greater for acetate than propionate or butyrate when these substrates were used for maintenance (Holter et al., 1970). Therefore, the use of a static k_L value may misrepresent underlying understanding of energy transformations. Consequently, the estimation of dietary NE_L may improve with models that predict HP by accounting for sources of energy substrates and end products formed. The objective of this study was to derive models that explain variation in HP of lactating Jersey cows. We hypothesized that HP could be estimated from MBW and DMI, and that the addition of variables that represent the nature of nutrients contained in feed consumed would further

explain variation by better representing the biological basis of energy transformations.

MATERIALS AND METHODS

Data Collection

Data from 9 research experiments conducted at the University of Nebraska–Lincoln's Dairy Metabolism Unit were used (Foth et al., 2015; Drehmel et al., 2018; Judy et al., 2018, 2019a,b; Knoell et al., 2019; Reynolds et al., 2019; Morris et al., 2020a,b). Across these 9 experiments, data from 293 animal-periods were collected on 54 Jersey cows. However, digestible energy (DE), and nutrient digestibility were not measured on all observations ($n = 261$ – 277 for the data set with DE and nutrient digestibility). In 2 studies (Judy et al., 2019a,b), a covariate period was conducted where DE, ME, and nutrient digestibility were not measured. Additionally, during the experimental period of Judy et

Table 1. Descriptive statistics of the data used for the analysis to estimate heat production of lactating Jersey cows

Item ¹	n	Mean	SD	Minimum	Median	Maximum
GE intake, Mcal/d	293	79.8	11.1	41.6	79.8	106.4
HP, Mcal/d	293	22.1	2.86	15.3	22.1	29.2
HP, % of GE intake	293	28.1	3.70	18.8	27.6	42.2
Animal descriptions						
DIM, d	293	182	72.3	44	174	410
Parity	293	3.0	0.95	2.0	3.0	5.0
BW, kg	293	453	44	342	452	568
Metabolic BW, kg ^{0.75}	293	98.2	7.2	79.5	98.0	116.4
BCS ²	272	3.27	0.35	2.00	3.25	4.25
DMI, kg/d	293	18.2	2.53	9.6	18.2	25.0
Milk and components yield						
Milk yield, kg/d	293	25.0	5.49	7.8	24.6	43.0
Milk yield, kg/kg of DMI	293	1.38	0.242	0.72	1.37	2.15
Fat, kg/d	293	1.40	0.292	0.48	1.39	2.19
Fat, kg/kg of DMI	293	0.0768	0.0127	0.0485	0.0766	0.116
Protein, kg/d	293	0.90	0.165	0.33	0.89	1.29
Protein, kg/kg of DMI	293	0.0493	0.0058	0.0332	0.0490	0.0701
Lactose, kg/d	290	1.20	0.285	0.33	1.19	2.10
Lactose, kg/kg of DMI	290	0.0658	0.0130	0.0339	0.0656	0.110
Digested energy and nutrients						
DE, Mcal/kg of DM	261	2.88	0.219	2.30	2.89	3.77
dCP, kg/d	277	2.25	0.404	1.32	2.21	3.39
CP digestibility, %	277	68.2	6.3	49.4	68.3	82.8
dNDF, kg/d	277	2.88	0.722	0.81	2.83	5.06
NDF digestibility, %	277	47.3	6.6	24.5	46.9	65.8
dSTA, kg/d	277	4.02	1.10	1.52	4.19	6.62
Starch digestibility, %	277	95.0	2.7	93.5	95.2	100.0
Urinary N excretion, g/d	261	188	57.4	56.9	182	394
Dietary composition, % of DM						
CP	285	17.7	0.95	15.2	17.7	19.5
NDF	285	31.9	3.51	25.5	32.0	43.0
Starch	285	25.0	3.48	16.2	25.8	31.1
Crude fat	281	4.2	0.74	2.2	4.2	6.4

¹HP = heat production; GE = gross energy; NE_M = net energy for maintenance [$0.100 \times$ metabolic BW (Moraes et al., 2015)]; DE = digestible energy; dCP = apparent digested CP; DE CP = digested energy from CP; dNDF = digested NDF; DE NDF = digested energy from NDF; dSTA = digested starch; DE STA = digested energy from starch.

²On a 1 to 5 scale.

al. (2019a), nutrient digestibility was measured, but, of the energy fractions variables, only HP was measured. Descriptive statistics for variables are listed in Table 1.

In all 9 experiments, O₂ consumption and CO₂ and CH₄ production were determined using headbox-type indirect calorimeters as described by Foth et al. (2015). Cows were housed in a temperature-controlled room (20°C) in tiestalls equipped with rubber mats. In all studies except for 1, cows were adapted to experimental diets for 21 or 28 d. In Judy et al. (2018), a 10-d adaptation period was used; however, in this study, experimental diets remained the same throughout the experiment, and only feeding frequency (once or twice per day) changed. In all experiments except for 1, a single group of cows were used. In Foth et al. (2015), cows were divided into 2 groups (termed block in the statistical model). All studies used a 23-h gas collection period that occurred after adaptation. All gas data were adjusted to a 24-h period. Gas data were collected for 1 or 2 d. For the data set where gas was collected for 2 d (n = 155), daily variation in HP was low (CV = 4.6%). Therefore, given our main objectives and the conditions of the current experiment, in which cattle were housed a climate-controlled tiestall facility, we believed that 1 d of gas collection was adequate to estimate HP for this study. Gas collection for 1 d may not be adequate when environmental conditions can vary or feed delivery is not held constant. Cows were fed within the headboxes and allowed free access to water via a water bowl. Details for the specific methods used to quantify gas consumption and production can be found in individual publications (Foth et al., 2015; Drehmel et al., 2018; Judy et al., 2018, 2019a,b; Knoell et al., 2019; Reynolds et al., 2019; Morris et al., 2020a,b). Heat production was estimated through calculation of observed O₂ consumption and CO₂ production with correction for CH₄ production and urinary N excretion according to Brouwer (1965) as follows:

$$\begin{aligned} \text{HP (Mcal)} = & 0.003866 \times \text{O}_2 \text{ (L)} + 0.001200 \\ & \times \text{CO}_2 \text{ (L)} - 0.000518 \times \text{CH}_4 \text{ (L)} \\ & - 0.001431 \times \text{urinary N (g)}. \end{aligned} \quad [1]$$

In all 9 experiments, milk production and composition were quantified for 4 consecutive days. Cows were milked twice per day and fed once per day in all experiments except in Morris et al. (2020b), where cows were milked 3 times per day, and Judy et al. (2018), where cows were fed once or twice per day. In all studies, fecal and urine output was quantified by total collection for 4 consecutive days. Chemical composition of feeds, refusals, and feces was determined by Cumberland Valley Analytical Services Inc. (Waynesboro, PA) except

for Foth et al. (2015) and Reynolds et al. (2019), where analyses were completed at the Ruminant Nutrition Laboratory of the University of Nebraska–Lincoln. Methods were similar across location and are described in individual publications (Foth et al., 2015; Drehmel et al., 2018; Judy et al., 2018, 2019a,b; Knoell et al., 2019; Reynolds et al., 2019; Morris et al., 2020a,b). Crossover experimental designs were used in all 9 experiments.

Model Derivation Procedure

Response variable was HP (Mcal/d). Models were fit in a hierarchical structure (Figure 1). The first level included individual models using the variable categories of DMI, milk, and digestibility. In the second level, milk or digestibility variables were combined with DMI, where milk yield was used as the milk variable and DE was used as the digestibility variable, and each variable was expressed as a function of DMI to minimize collinearity. In the third level, the constituents of milk yield (fat, protein, and lactose) and DE (digested CP, NDF, and starch) were used with all variables expressed as a function of DMI. To calculate DE from digested nutrients, we multiplied digested CP, NDF, and starch (kg) by their corresponding enthalpies of 5.65, 4.2, and 4.23 Mcal/kg, respectively (NRC, 2001). This resulted in 7 models for each response variable. Specifically, models are as follows, with reference names for each model listed parenthetically in bold: (1) DMI (**INT**); (2) milk fat, protein, and lactose yield (**MILK-COMP**); (3) DMI and milk yield (**INT+MY**); (4) DMI and MILKCOMP variables as a function of DMI (**INT+MILKCOMP**); (5) daily intake of digested NDF (**dNDF**), CP (**dCP**), and starch (**dSTA**; **DIG**); (6) DMI and DE (**INT+DE**); and (7) DMI and NDF, CP, and starch digestibility (**INT+DIG**). An eighth model was fit to determine HP associated with urinary N excretion that accounted for DMI and milk fat, protein, and lactose yields as a function of DMI (**INT+MILKCOMP+UN**). The MBW was included in all models to estimate HP. As discussed previously, although forage inclusion (specifically forage NDF) can affect HP (Reynolds et al., 1991), it was not evaluated in the current experiment because in most studies the forage NDF was similar across treatments; consequently, differences between treatments was small (mean ± SD; 22.4 ± 2.28%). Initially, models with DMI included BCS and DIM; however, neither BCS nor DIM were significant, thus neither were included in derivation of final models. Fatty acid digestibility was only measured in 3 studies (n = 87), and its effects were not further explored.

Models were fit in R (version 3.5.2) with the lmer function (Kuznetsova et al., 2017). To account for the

variation associated with using individual animal observations, all models included the random effects of study ($n = 9$), cow ($n = 55$), and period within block within study ($n = 36$). If parameter estimates were close to 0 and nonsignificant ($P > 0.15$), the corresponding explanatory variables were removed from the model.

Model Evaluation

Simple correlation coefficients among all variables were assessed (Table 2). These correlation coefficients were used to assess potential multicollinearity among explanatory variables and used to aid in the explanation of observed parameters. In final models, multicollinearity among variables was assessed by variance inflation factor (Roman-Garcia et al., 2016), which was less than 5 for all variables, and in most cases less than 2. This indicated that the inflation in variance due to multicollinearity was minimal in the models presented.

To compare among models with the same response variables, concordance correlation coefficients (CCC; Lin, 1989) were calculated from predicted values with (CCC) or without (uCCC) adjustment for study, cow, and period within block within study. Concordance correlation coefficients assess both accuracy and precision of models. Because the CCC value includes the random intercept terms for each random effect, they typically produce more favorable values compared with uCCC (White et al., 2017a). When mixed-effects models are

used in an uninformed setting, the random effects will not be known; therefore, removal of the random effects, although not a statistically accurate depiction of model fit, is conducted to provide information on model fit when using the model for future use in naïve settings (White et al., 2017a). Furthermore, for each model, we reported the estimated standard deviation for cow ($\hat{\sigma}_c$), study ($\hat{\sigma}_s$), and error ($\hat{\sigma}_e$), which is more appropriate than the root mean squared error for evaluating mixed effect models (Boerman et al., 2015). The units for all $\hat{\sigma}$ values were the same as the response variable (Mcal/d).

The objective of the current study was to explain variation in HP rather than to develop a model that would definitively predict HP. We explored generating a prediction error of models using a Monte Carlo cross-validation as described by White et al. (2017b); however, the current data set only contained 9 studies that differ greatly by DIM, DMI, milk production, and dietary chemical composition. This resulted in prediction errors, slope, and intercept biases that were affected by which studies were selected by the Monte Carlo simulation. Therefore, results from the cross-validation may be misleading and are not reported herein.

RESULTS AND DISCUSSION

The number of observations for each variable tested were between 261 and 293 (Table 1). Average HP was

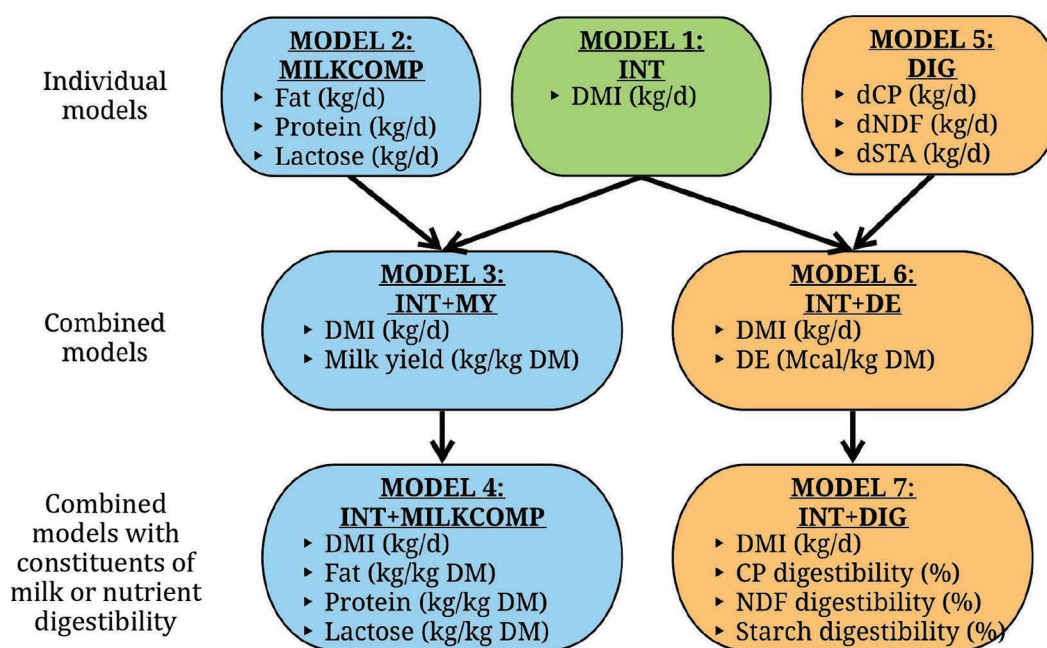


Figure 1. Illustration of 7 models that were fit for heat production. Models for heat production included metabolic BW. dCP = digested CP; dNDF = digested NDF; dSTA = digested starch; DE = digestible energy.

Table 2. Simple correlation coefficients among heat production, animal description, milk yield and components, and digestibility variables included in model development¹

Item	Variable																		
	MBW	DMI	MY	MY/DMI	Fat	Fat/DMI	Pro	Pro/DMI	Lact	Lact/DMI	DE/DMI	dCP	CP digestibility	dNDF	NDF digestibility	dSTA	Starch digestibility	UN	
HP	0.26*	0.68*	0.50*	0.09	0.40*	-0.08	0.59*	0.12*	0.49*	0.10	-0.14*	0.43*	-0.21*	0.38*	0.07	0.32*	0.15*	0.01	
MBW		0.20*	-0.05	-0.26*	0.03	-0.17*	0.07	-0.16*	-0.09	-0.28*	0.06	0.13*	0.04	-0.03	-0.13*	0.30*	0.00	0.16*	
DMI			0.63*	0.01	0.63*	-0.03	0.78*	0.08	0.60*	0.03	-0.05	0.58*	-0.30*	0.55*	0.09	0.54*	-0.02	-0.02	
MY				0.77*	0.78*	0.48*	0.86*	0.64*	0.99*	0.78*	-0.05	0.25*	-0.39*	0.21*	-0.01	0.47*	0.12*	-0.18*	
MY/DMI					0.50*	0.66*	0.48*	0.78*	0.79*	0.99*	-0.03	-0.13*	-0.25*	-0.16*	-0.09	0.16*	0.17*	-0.18*	
Fat						0.76*	0.77*	0.50*	0.75*	0.49*	-0.03	0.22*	-0.40*	0.16*	-0.11	0.53*	0.01	-0.03	
Fat/DMI							0.34*	0.60*	0.47*	0.63*	0.01	-0.18*	-0.25*	-0.24*	-0.21*	0.21*	0.02	0.00	
Pro								0.67*	0.83*	0.47*	-0.06	0.40*	-0.33*	0.28*	-0.01	0.57*	0.03	-0.09	
Pro/DMI									0.63*	0.75*	-0.04	-0.04	-0.17*	-0.18*	-0.13*	0.26*	0.07	-0.10	
Lact										0.81*	-0.05	0.25*	-0.36*	0.22*	0.02	0.42*	0.13*	-0.18*	
Lact/DMI											-0.03	-0.08	-0.22*	-0.10	-0.04	0.12	0.16*	-0.18*	
DE/DM												0.37*	0.55*	0.18*	0.34*	-0.12	0.08	0.08	
dCP													0.54*	0.49*	0.27*	0.06	-0.04	0.41*	
CP														0.04	0.30*	-0.44*	-0.02	0.50*	
digestibility																			
dNDF																			
NDF																			
digestibility																			
dSTA																			
Starch																			
digestibility																			

¹Items are repeated horizontally and vertically in the same order and the same units. HP = heat production (Mcal); MBW = metabolic BW (kg^{0.75}); DMI (kg/d); MY = milk yield (kg/d); MY/DMI = milk yield/DMI (kg/kg); Fat = milk fat yield (kg/d); fat/DMI = milk fat yield/DMI (kg/kg); pro = milk protein yield (kg/d); pro/DMI = milk protein yield/DMI (kg/kg); lact = milk lactose yield (kg/d); lact/DMI = milk lactose yield/DMI (kg/kg); DE/DMI = digested energy (Mcal/kg of DM); dCP = apparent digested CP (kg/d); CP digestibility (%); dNDF = digested NDF (kg/d), NDF digestibility (%); dSTA = digested starch (kg/d); starch digestibility (%); UN = urinary N excretion (g/d).

* *P* < 0.05.

22.1 ± 2.86 Mcal/d. The data set included cows with a wide range in DIM (44–410), DMI (9.6–25.0 kg/d), and milk yield (7.8–43.0 kg/d).

Residual versus predicted plots for all HP models are reported in Supplemental Figure S1 (<https://doi.org/10.3168/jds.2020-18976>). Although a slope bias was observed ($P < 0.10$) for some models, the magnitude was less than 2% of error variance in all cases, and was thus not a concern.

Factors that Affect HP

Heat arises from the inefficiency in the conversion of a substrate into a product and from the complete oxidation of a substrate (Baldwin, 1995); it is commonly estimated in ruminants using the Brouwer (1965) equation. Negative coefficients are included in the Brouwer equation for urinary N excretion because protein oxidation leads to urinary urea excretion, and thus protein oxidation is not complete. Therefore, O_2 and CO_2 associated with this incomplete oxidation must be accounted for when estimating HP (McLean and Tobin, 1987). Total HP is an aggregate of heat for basal metabolism, activity, digestion and absorption, fermentation, product formation, thermoregulation, and waste formation and excretion (NRC, 1981). We hypothesized that MBW and DMI could predict HP. Furthermore, we predicted that the addition of milk component yield, digestibility of nutrients, and urinary N excretion would explain more variation in HP by decreasing $\hat{\sigma}_e$ and increasing CCC. Specifically, we expected the following: (1) MBW to account for the NE_M component of HP; (2) DMI to indirectly account for the digestion and absorption, fermentation, and product formation component of HP; (3) milk fat, protein, and lactose yield to account for heat of production formation; (4) digested NDF, CP, and starch to account for heat of digestion and absorption, and fermentation; and (5) urinary N excretion to account for heat associated with waste formation and excretion, and protein catabolism.

In agreement with our hypothesis, INT explained most of the variation in HP ($uCCC = 0.84$, and $\hat{\sigma}_e = 1.38$; Table 3). However, counter to our hypothesis, the addition of nutrient digestibility and milk component yield did not improve our ability to explain variation in HP based on similar $uCCC$ and $\hat{\sigma}_e$. A lack of improvement in model performance with inclusion of nutrient digestibility and milk component yield may have occurred because most of the variation in HP in the current study was explained by MBW and DMI. Furthermore, no difference in model performance would suggest that similar variation was explained by milk component yield or digested nutrients compared with DMI, which

is not surprising given the correlation between most of these variables ($r > 0.55$; $P < 0.05$; Table 2). The relationship between HP and other response variables may improve our understanding of biological sources of variation in HP.

Given the other variables included in the models, increasing MBW increased HP on average by 0.111 to 0.165 Mcal per unit of MBW (Table 3). Because basal metabolism is a function of MBW (Brody, 1945; Kleiber, 1975), MBW was expected to account for a large fraction of the variation in HP. The MILKCOMP and DIG models, which did not include DMI, resulted in MBW coefficients of 0.165 and 0.147. These values are likely larger than actual NE_M , and thus demonstrate the importance of accounting for DMI when explaining variation in HP. The MILKCOMP and DIG models aside, our average MBW coefficient was 0.122 Mcal, which is 53% greater than the current NE_M value used by NRC (2001). However, Moraes et al. (2015) recently reported that NE_M has increased over time from 0.074 to 0.124 for measurements taken during 1963 to 1973, and 1984 to 1995, respectively. From 935 observations from European calorimetry studies published between 1992 to 2010, NE_M averaged 0.105 Mcal/MBW (Dong et al., 2015). Most of the historical energetics data were collected on Holsteins cows; however, energy utilization and maintenance energy requirements did not differ between Holsteins and Norwegian, Jersey \times Holstein, or Norwegian \times Holstein cows (Dong et al., 2015).

On average, increasing DMI increased HP by 0.560 to 0.600 Mcal/kg. Increased DMI typically corresponded with increased HP, which has been previously observed (Purwanto et al., 1990; Reynolds et al., 1991). Up to 50% of total body O_2 consumption in ruminants can be attributed to metabolism in the gastrointestinal tract and liver (Seal and Reynolds, 1993). In sheep, increasing DMI increased digestive tract and organ weight as a proportion of BW (McLeod and Baldwin, 2000). In growing heifers, increased DMI increased total O_2 consumption by the portal-drained viscera and liver (Reynolds et al., 1991). Additionally, DMI was correlated with milk production ($r = 0.63$; Table 2); therefore, a strong relationship between DMI and HP was not surprising.

Synthesis of milk constituents is a major contributor to the HI of lactating cows. Although empirical models do not directly measure the underlying mechanistic nature of biology (Baldwin, 1995), interpretation of parameter estimates may be useful in determining the relationship between response and explanatory variables. When accounting for MBW and DMI, HP increased on average by 1.54 ± 0.57 Mcal per unit increase in milk yield over DMI (kg/kg of DMI); therefore, we were interested in partitioning the HP associated with MY

Table 3. Parameter estimates and fit statistics for models to predict heat production (Mcal/d) of Jersey cows from metabolic BW (MBW) plus DMI (INT); milk fat, protein, and lactose yield (MILKCOMP); INT plus milk yield (INT+MY); INT plus MILKCOMP variables as a function of DMI (INT+MILKCOMP); digested NDF, CP, and starch (DIG); INT plus digested energy (INT+DE); or INT plus NDF, CP, and starch digestibility (INT+DIG)

Item	INT		MILKCOMP		INT+MY		INT+MILKCOMP		DIG		INT+DE		INT+DIG	
	Value	SE	Value	SE	Value	SE	Value	SE	Value	SE	Value	SE	Value	SE
Model	1		2		3		4		5		6		7	
Variable ¹														
Intercept	-0.198 ^a	1.80	-2.30 ^a	1.90	-3.52	2.16	-4.78	2.25	0.719 ^a	2.02	5.02	2.58	-2.34	4.84
MBW, kg ^{0.75}	0.122	0.018	0.165	0.018	0.129	0.018	0.132	0.018	0.147	0.020	0.114	0.020	0.111	0.019
DMI, kg/d	0.560	0.048			0.591	0.48	0.577	0.047			0.598	0.051	0.600	0.048
Milk fat, kg/d			1.83	0.66										
Milk protein, kg/d			6.17	1.13										
Milk yield, kg/kg of DMI					1.54	0.57								
Milk fat, kg/kg of DMI							16.4	12.0						
Milk protein, kg/kg of DMI							40.2	23.0						
dCP, kg/d									1.63	0.37				
dSTA, kg/d									0.762	0.167				
DE, Mcal/kg of DM											-1.72	0.59		
CP digestibility, %													-0.0432	0.027
NDF digestibility, %													-0.0666	0.018
Starch digestibility, %													0.0910	0.046
Fit statistics ²														
n	293		293		293		293		277		261		277	
BIC	1,161		1,178		1,159		1,148		1,157		1,045		1,118	
CCC	0.89		0.88		0.89		0.89		0.86		0.89		0.90	
uCCC	0.84		0.81		0.85		0.84		0.79		0.85		0.84	
$\hat{\sigma}_e$	0.61		0.60		0.59		0.56		0.68		0.62		0.64	
$\hat{\sigma}_s$	1.59		1.82		1.51		1.62		2.02		1.47		1.63	
$\hat{\sigma}_c$	1.38		1.44		1.36		1.37		1.52		1.38		1.33	

^aNot different from 0 ($P > 0.20$).

¹MBW = $BW^{0.75}$; dCP = apparent digested CP; dSTA = digested starch; dNDF = digested NDF.

²n = number of observations; CCC = concordance correlation coefficient; BIC = Bayesian information criterion; uCCC = concordance correlation coefficient without random effects adjustment; $\hat{\sigma}_e$ = square root of the estimated variance associated with cow (Mcal); $\hat{\sigma}_s$ = square root of the estimated variance associated with study (Mcal); $\hat{\sigma}_c$ = square root of the estimated variance associated with error (Mcal).

into HP due to fat, protein, or lactose synthesis. For the MILKCOMP and INT+MILKCOMP models to estimate HP, the parameter estimate for milk lactose yield was not different from 0 ($P > 0.27$), and was consequently removed from the final model. Although synthesis of milk lactose results in HP, milk lactose was highly correlated with milk fat ($r = 0.75$) and milk protein ($r = 0.83$; Table 2); therefore, changes in milk fat and protein yield likely explained the variation in HP that arose from changes in milk lactose yield. The parameter estimate for milk protein was 2-fold greater than that of milk fat when expressed on a kg/d (6.17 ± 1.13 vs. 1.83 ± 0.656) or kg/kg of DMI basis (40.2 ± 23.0 vs. 16.4 ± 12.0 ; Table 3). This difference may be explained by a greater energetic efficiency for synthesizing milk fat compared with milk protein. De novo synthesis of milk fat is about 0.70 efficient (Dado et al., 1993); whereas, conversion of dietary fat or tissue fat into milk fat has an energetic efficiency of 0.94 to 0.97 (Baldwin et al., 1985). Given that milk fat is 50% dietary or tissue in origin (Bauman and Grinari, 2003), efficiency of milk fat synthesis is 0.83. Synthesis of milk protein is estimated to require approximately 2 Mcal of ME/kg (Dado et al., 1993), and thus the theoretical maximum efficiency of milk protein synthesis is 0.74. However, because of protein turnover, actual protein synthesis in mammary glands will always exceed milk protein yield. Estimated rates of protein turnover range from 140% of milk protein yield in lactating dairy cows (Lemosquet et al., 2010) to 300% of milk protein yield in lactating dairy goats (Hanigan et al., 2009), with the prediction depending on which labeled AA was used for quantification. When accounting for the fact that actual protein synthesis is 40 to 200% greater than milk protein yield, energetic efficiency of milk protein synthesis ranges from 0.48 to 0.67. Consequently, milk fat production will lead to a lower HI compared with milk protein synthesis.

Increasing the supply of digested nutrients was expected to increase HP because of the underlying correlation with DMI. However, digestion of NDF and starch gives rise to different VFA profiles, HI associated with intermediary metabolism differs by VFA (Holter et al., 1970), and catabolism of absorbed AA contributes to HI (Reynolds, 2006). Therefore, we expected to see differences in HP associated with digested NDF, CP, and starch. The parameter estimates for dNDF (kg/d) in the DIG HP model were not different from 0 (0.146 ± 0.242 Mcal/kg; $P = 0.55$), and thus were removed from the final model. Because heat of fermentation is a component of HP (NRC, 1981) and NDF is primarily digested via ruminal fermentation, we were surprised that the effect of dNDF on HP was small. However,

dNDF was correlated with dCP ($r = 0.49$) and dSTA ($r = -0.19$; Table 2); therefore, variation in HP associated with dNDF was likely explained by dCP and dSTA. Furthermore, in the data set used in the current study, change in dietary NDF content was primarily driven by changes in byproduct inclusion ($r = 0.83$ for dietary NDF and nonforage NDF). It is likely that nonforage NDF does not stimulate a similar increase in HP as does increasing forage inclusion (Reynolds et al., 1991). Dietary NDF content, rather than digestible NDF, may be a better variable for explaining variation in HP. Therefore, we tested the effects of dietary NDF content in place of NDF digestibility. When dietary NDF content replaced dNDF in the DIG model, HP increased by 0.221 ± 0.0587 Mcal per percentage unit increase in dietary NDF on average (data not shown). Additionally, for the DIG HP model, both dCP and dSTA were associated with HP when MBW was included (Table 3). For the DIG HP model, the coefficient for dCP was almost 2-fold that of dSTA (1.34 ± 0.372 vs. 0.762 ± 0.167 Mcal/kg; Table 3). An increase in HP with increased dCP was expected. Tyrrell et al. (1970) reported that feeding CP in excess of requirements resulted in decreased NE_t , which may be attributable to an increase in HP associated with metabolizing excess CP and transforming DE into urinary energy (Reed et al., 2017). The HP associated with excess N may originate from ureagenesis or AA catabolism (see discussion on the effects of urinary N excretion on HP and HI). Most dietary starch is digested to VFA in the rumen and will subsequently be used as an energy source for the body or be converted into products. Our results suggest that a greater quantity of HP is associated with each kilogram of dCP compared with dSTA, which supports research conducted over 100 yr ago by Rubner, who observed that the HP associated with oxidation of protein is greater than fat or carbohydrates (Kleiber, 1975).

Additional digestibility models were fit that included DE and digestibility of CP, NDF, and starch. We expected INT+DE and INT+DIG to improve model performance compared with INT; however, as previously discussed, these models resulted in similar uCCC and $\hat{\sigma}_e$ values. For the INT+DE model to estimate HP, increasing DE (Mcal/kg of DM) decreased HP (-1.72 ± 0.592 Mcal). In the current database, DE content was positively correlated ($r = 0.25$) with dietary crude fat and negatively correlated ($r = -0.29$) with dietary NDF content (data not shown). As discussed previously, increased dietary fat and decreased NDF should result in a diet that will lead to less HP. For the INT+DIG HP model, decreased HP was observed with increased digestibility of CP and NDF (Mcal/%; -0.0432 ± 0.27

and -0.0666 ± 0.018); as starch digestibility increased, HP increased on average by 0.0910 ± 0.046 Mcal/%. Starch digestibility was positively correlated with milk and lactose yield (Table 2), which will lead to increased HP. Negative coefficients for CP and NDF digestibility may have occurred because CP digestibility were negatively correlated ($r < -0.25$) with DMI and milk component yields, and NDF digestibility was negatively correlated ($r = -0.13$) with MBW. As NDF digestibility increased, energy expenditure associated with digestion, and HP from mass of ruminal tissue may have decreased because of changes in the source of NDF (Reynolds et al., 1991; Cantalapiedra-Hijar et al., 2014). Additionally, at a constant DMI, increasing NDF and CP digestibility may increase the partitioning of energy toward milk and away from heat, leading to decreased HP.

The Effects of Urinary N Excretion on HP and Increment

Feeding excess protein to dairy cows increases HP and decreases energy balance (Tyrrell et al., 1970; Reed et al., 2017). Urinary N excretion can serve as an indicator of AA oxidation, and thus excess protein; therefore we hypothesized that the inclusion of urinary N excretion could improve our ability to explain variation in HP and HI. Compared with other models for HP and HI, the models that included urinary N excretion had similar uCCC (0.83) and $\hat{\sigma}_e$ values (1.40 Mcal; Table 4). Overall, partitioning of the variation in HP was not improved with the inclusion of urinary N excretion.

A secondary objective of determining the relationship between HP and urinary N excretion was to quantify the contribution of protein catabolism to heat energy. On average, when accounting for MBW, DMI, milk fat yield, and milk protein yield, HP increased by 5.32 ± 2.43 Mcal/kg of urinary N excretion. In an analysis of a historical indirect calorimetry data set, Reed et al. (2017) determined that HP was associated with excess N intake, which was defined as the digested N supply minus N requirements for maintenance, milk production, and pregnancy as defined by NRC, (2001). In the Reed et al. (2017) analysis, HP increased from 6.5 to 7.6 Mcal/kg of excess N when accounting for energy intake, MBW, and milk energy output. Coefficients from the Reed et al. (2017) analysis are larger than ours, which is likely because some urinary N excretion is a function of maintenance and milk production (NRC, 2001). Consequently, metabolic fecal N was subtracted out as a component of fecal N excretion and maintenance N requirements, thus underestimating excess N. Both will lead to a greater coefficient than the method used in the current study. In lactating dairy cows, the

primary form of urinary N is urea (Spek et al., 2013), and the energetic cost of ureagenesis from ammonia is estimated to be 3.8 Mcal/kg of N (Martin and Blaxter, 1965). Ureagenesis occurs as a result of catabolism of AA by rumen microbes, catabolism of AA that are supplied in excess of requirements, and turnover of body protein stores (Lobley, 1992; Firkins and Reynolds, 2005; Reynolds, 2006). Reynolds (2006) suggests that ureagenesis may not be the primary contributor to increased HP with excess protein intake; rather, catabolism of AA leads to increased HP with increase CP intake. As described by Firkins and Reynolds (2005), because ruminants are evolutionarily adapted to be dependent on urea recycling, a large energetic cost to ureagenesis would be constrictive to urea recycling. Supporting evidence includes that increasing ammonia supply or feeding urea does not reduce milk yield (Moorby and Theobald, 1999) or increase liver O₂ consumption (Lobley et al., 1995; Firkins and Reynolds, 2005). The HP that was associated with UN in the current experiment on average was 1.0 Mcal/d (1.3% of GE intake). In the current study, urinary N excretion explained variation in HP that was associated with the catabolism of protein.

Due to the amount of heat associated with urinary N excretion, the question arises: will increasing dietary

Table 4. Parameter estimates and fit statistics for models to predict heat production (Mcal/d) of Jersey cows from metabolic BW (MBW; heat production only); DMI; milk fat, protein, and lactose yield; and urinary N excretion¹

Item	Heat production	
	Value	SE
Variable ¹		
Intercept	-5.30	2.28
MBW, kg ^{0.75}	0.120	0.19
DMI, kg/d	0.602	0.52
Milk fat, kg/kg DMI	18.6	12.5
Milk protein, kg/kg DMI	46.4	24.1
Urinary N excretion, kg/d	5.32	2.43
Fit statistics ²		
n		261
BIC		1,030
CCC		0.89
uCCC		0.84
$\hat{\sigma}_c$		0.52
$\hat{\sigma}_s$		1.65
$\hat{\sigma}_e$		1.39

¹MBW = BW^{0.75}.

²n = number of observations; BIC = Bayesian information criterion; CCC = concordance correlation coefficient; uCCC = concordance correlation coefficient without random effects adjustment; $\hat{\sigma}_c$ = square root of the estimated variance associated with cow (Mcal); $\hat{\sigma}_s$ = square root of the estimated variance associated with study (Mcal); $\hat{\sigma}_e$ = square root of the estimated variance associated with error (Mcal).

CP above requirements to replace carbohydrates decrease NE_L supply? Assuming a true digestibility of dietary CP of 85% (NRC, 2001) and that all dietary CP is excreted as urinary N, the HP associated with urinary N excretion is 0.72 Mcal/kg of CP. Additionally, N from excess CP is primarily excreted as urea in urinary N (Spek et al., 2013), which has an enthalpy of 5.4 Mcal/kg of N or 0.86 Mcal/kg of CP. Thus, the sum of energy associated with increased HP and urinary energy excretion from feeding CP as an energy source is 1.6 Mcal/kg. This is similar to the difference in enthalpy between CP and carbohydrates (5.6 vs. 4.2 Mcal/kg; NRC, 2001); therefore, differences in energy supply between feeding CP or carbohydrates is dependent on digestibility of the CP or carbohydrate source. Average true digestibility of CP is slightly less than starch (85 vs. 92%), but true digestibility of CP is much greater than NDF (NRC, 2001; Ferraretto et al., 2013). Thus, replacing dietary NDF with CP may improve NE_L supply.

CONCLUSIONS

From 293 individual animal observations on lactating Jersey cows, HP averaged 22.1 ± 2.86 Mcal/d or $28.1 \pm 3.70\%$ of GE intake. Our results suggest that variation in HP is explained by MBW and DMI. Counter to our hypothesis, the inclusion of milk component yield and nutrient digestibility did not improve our ability to explain variation in HP and HI. Parameter estimates from these models agree with other biological and biochemical estimates of energy transaction in lactating cows. For example, HP associated with milk protein synthesis was approximately 2-fold that of milk fat synthesis. Additionally, for every kilogram of urinary N excreted, HP increased on average by 5.32 Mcal.

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